Quaternary Bats from the Impossível-Ioiô Cave System (Chapada Diamantina, Brazil): Humeral Remains and the First Fossil Record of *Noctilio leporinus* (Chiroptera, Noctilionidae) from South America

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ABSTRACT

The partially submerged Impossível-Ioiô cave system located in the karst region of Chapada Diamantina in Bahia (Brazil) has recently been the target of extensive paleontological studies. Here we provide the first report of fossil bats from this cave system, in which we recognize six species based on humeral remains: *Furipterus horrens*, *Chrotopterus auritus*, *Mormoops* cf. *megalophylla*, *Pteronotus gymnonotus*, *Pteronotus parnellii*, and *Noctilio leporinus*. Morphology of the humerus of these taxa is described in a comparative framework to document taxonomic assessments and provide a basis for future studies of fossil bat faunas. The relevance of the new records reported here is evaluated at a broader continental scale, as well as in contrast with the recent bat fauna of the region. The record of *Noctilio leporinus* stands as the first fossil occurrence of this species on the South American continent.

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INTRODUCTION

The Chapada Diamantina plateau, located in the state of Bahia and extending northeast of the Espinhaço mountain chain, is one of the most important karst areas in Brazil (fig. 1). The north-central region of the plateau is well known for its many caves, some of which are filled by crystal waters and most of which remain unexplored, with great potential for geopaleontological studies. During the last few years we have carried out extensive paleontological research in this region centered on the Impossível-Ioiô cave system and focused on underwater Quaternary deposits rich in fossil mammals. A variety of small and medium-sized mammals have been found in this system and, aside from a skeleton of †*Nothrotherium* sp. (Xenarthra: Nothrotheriidae) (Perini et al., in prep.), all of the records represent extant taxa. This contribution is the first report describing the bat paleofauna recovered from the Impossível-Ioiô, which is the fifth site with bat remains known for the Chapada Diamantina plateau (Cartelle and Abuhid, 1994; Czaplewski and Cartelle, 1998).

Previous knowledge of the bat paleofauna of the Quaternary of Chapada Diamantina is based on reports by Cartelle and Abuhid (1994) and Czaplewski and Cartelle (1998), who summarized data from four caves (fig. 1): Toca da Boa Vista (10°09′36.72″S, 40°51′38.88″W), Toca da Barriguda (10°08′26.88″S, 40°51′07.92″W), Gruta dos Brejões (10°59′10.32″S, 41°25′59.52″W), and Toca dos Ossos (10°55′49.44″S, 41°03′27.36″W). Czaplewski and Cartelle (1998) proposed a formal time reference based on a sample of *Mormoops megalophylla* from Toca da Boa Vista that was radiocarbon dated at approximately 20,000 years BP. Toca da Boa Vista, the largest cave in Brazil, preserves by far the most diverse regional bat paleofauna with 19 species records, followed by Gruta dos Brejões with 10 bat species. Only one of the 27 taxa recovered from this set of caves is extinct: †*Desmodus draculae*, the giant vampire bat.

The paleofauna of bats from Chapada Diamantina is addressed here in the context of the new records from Impossível-Ioiô, including the first Quaternary records of *Noctilio leporinus* from South America. This first report is exclusively based on humeral remains, which are diagnostic at the species level in Chiroptera (see below); other osteological data will be presented in a planned series of additional contributions on the fossil bats from this region. The relevance of the new records reported here is evaluated at a broader continental scale, as well as in contrast with the recent bat fauna of the region (e.g., Sbragia, 2012). The current study contributes to ongoing efforts to shed new light on the Pleistocene/Holocene bats of the South American continent, and more specifically to better understand the evolution of faunas of the unique karst region of northeastern Brazil, currently covered by semiarid savannas within the Caatinga domain.

MATERIAL AND METHODS

STUDY AREA AND GEOLOGICAL BACKGROUND

The Ioiô-Impossível (12°23′13.56″S, 41°32′57.48″W) is a large cave system located in the Iraquara karst region (Laureano and Cruz, 2002; Laureano, 1998; Cruz, 1998) (fig. 1), a subunit of the Precambrian carbonate rocks of the Ulna Group (Auler and Farrant, 1996) situ-
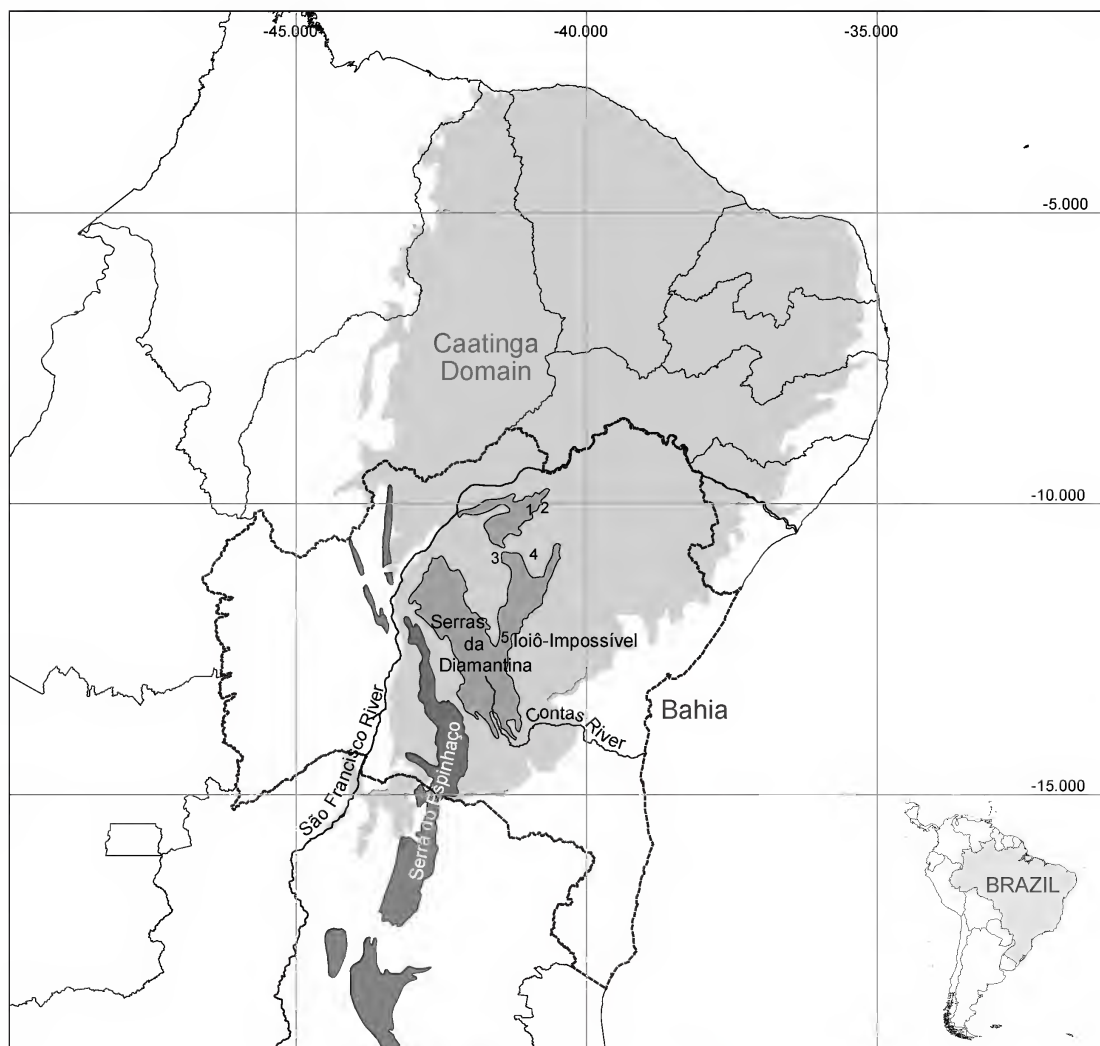
FIGURE 1. Map illustrating northeastern Brazil. Light gray shading indicates the extent of the Caatinga Biome, dark gray the Serra do Espinhaço mountains, and medium gray shading shows the extent of the Serras da Diamantina plateau. Numbers indicate locations of caves from which fossil bats have been collected: **1,** Toca da Boa Vista; **2,** Toca da Barriguda; **3,** Gruta dos Brejões; **4,** Toca dos Ossos; and **5,** the new fossil site Ioiô-Impossível.

ated in the geologically well-known Irecê sedimentary basin (Souza et al., 1993). Paleontological explorations carried out in this cave have been concentrated on the main ducts, which are partially filled with water. These ducts can be accessed via the Impossível main entrance, which is situated at the bottom of a collapsed sinkhole that is oval in shape and approximately 100 m in diameter and 50 m in height (fig. 2). The cave ducts are partially filled by sediments that contain concentrations of fossil vertebrate bones in some locations, mostly medium-sized animals such as carnivores (Felidae, Procyonidae, Mustelidae) and xenarthrans (Dasypodidae, Myrmecophagidae).

FIGURE 2. Photograph showing one of the openings of the Ioiô-Impossível cave system as viewed from the top edge of the sinkhole. The main opening to the "*Nothrotherium* duct" is indicated by a dashed arrow.

Many of the medium-sized and larger specimens found in the bone concentrations are disarticulated, but nearly all are spatially arranged in such way that they seem to have maintained, at least to some extent, their anatomical relationships. This suggests that very little bone displacement occurred after the death of these animals, which in turn implies that the flux of water and sediments has been very slow and without sufficient energy to disperse larger bones along the cave ducts. A complete analysis of the taphonomy of these fossils will be the subject of another work, but the most likely hypothesis is that these nonvolant animals fell into the cave system via skylights, small holes, and fissures (all present in the area) that can function as pitfalls, and that they were preserved near where they died or their carcasses came to rest (Hubbe et al., 2011). In contrast, the isolated microvertebrate remains recovered in the cave system do not present evidence of the conditions described above, seeming instead to have been accumulated as a mix of
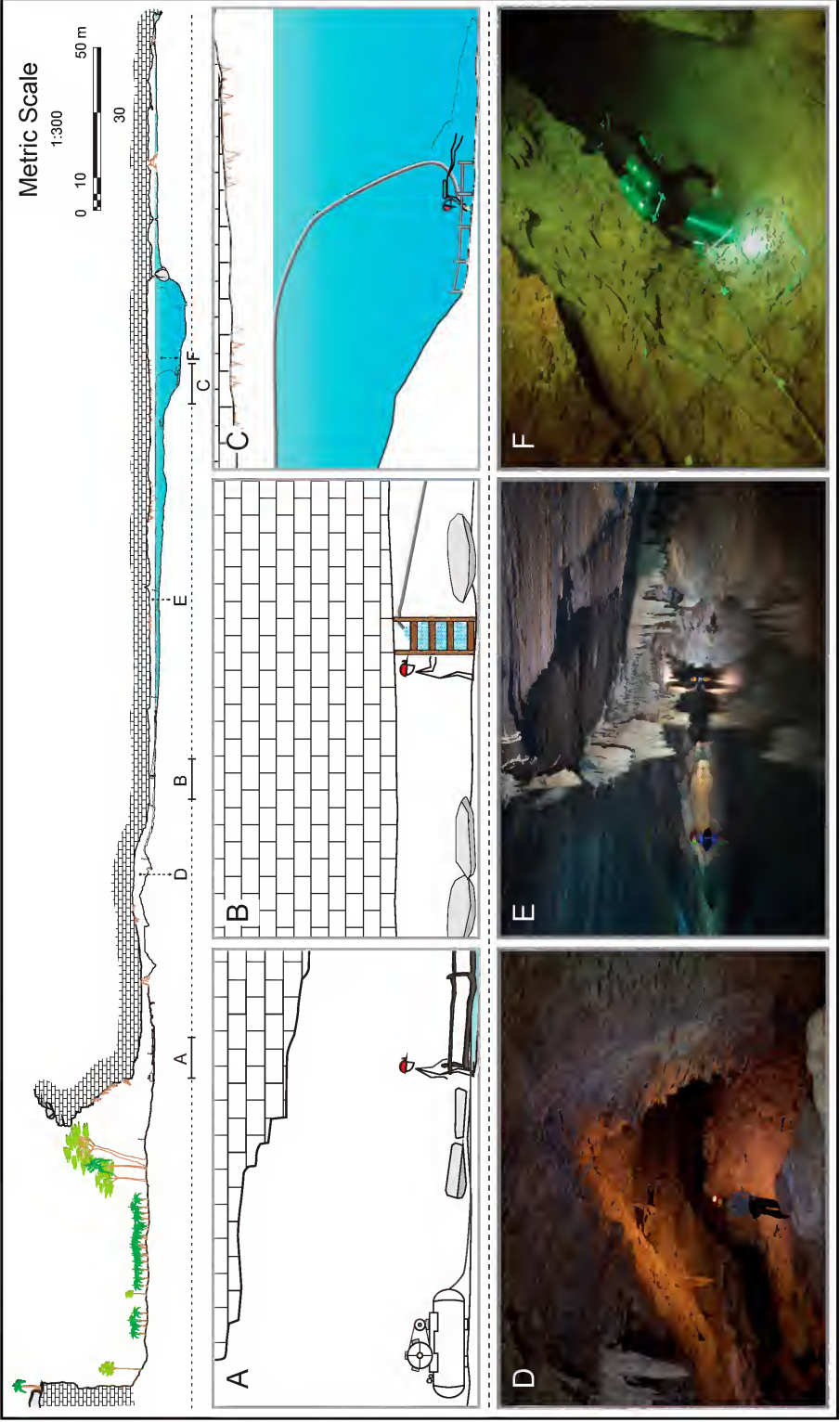
FIGURE 3. Cross section of the "*Nothrotherium* duct" with schematics showing the airlift system used to collect fossils of microvertebrates including bats: (A) air-compression system placed at the cave entrance; (B) sieve system; and (C) at the *Nothrotherium* grid, a diver operating the pipe end with valve control for the air injection, which sucks water and sediments through the main pipe to the sieve system. Photographs below show images of the "*Nothrotherium* duct": (D) dry area approximately 50 m from the entrance; (E) waterlogged portion approximately 150 m from the entrance; and (F) underwater view of the *Nothrotherium* grid.

TABLE 1. Measurements of humeri of fossil bats from the Impossível-Ioiô cave system. Measurements follow standards described by Czaplewski and Cartelle (1998) and are in mm.

Abbreviations are as follows: **MN,** Museu Nacional (Rio de Janeiro) catalog number; **ch,** complete humerus; **ps,** proximal end of humerus with shaft; **p,** proximal end only; **ds,** distal end of humerus with shaft; **d,** distal end only; **TL,** total length; **SD,** shaft diameter; **WP,** width of proximal end of humurus; **WD,** width of distal end of humerus; *, measurement approximate due to damage.

MN	Species	Description	TL	SD	WP	WD
57400	*Noctilio leporinus*	ch	39.94	2.52	6.37	6.66
57401		ch	39.13	2.51	5.95	6.43
57402	*Mormoops cf. megalophylla*	ch	31.45	1.8	3.94	4.26
57403		ch	31.76	1.87	4.07	4.57
57404		ps	–	1.81	4.05	–
57405		ps	–	1.94	4.12	–
57406		ch	31.14	1.74	4.07	4.45
57407		ch	30.74	1.8	4.08	4.17
57408		ds	–	1.81	–	4.59
57409		ds	–	1.67	–	3.62
57410		ps	–	1.77	4.05	–
57411	*Pteronotus gymnonotus*	ch	26.72	1.46	3.82	3.68
57412		ds	–	1.43	–	3.87
57413		ch	28.55	1.53	3.95	3.84
57414		ds	–	1.37	–	3.68
57415		ds	–	1.37	–	3.76
57416		ps	–	1.46	3.9	–
7417		p	–	–	3.59*	–
57418	*Pteronotus parnellii*	ds	–	1.54	–	4.45
57419		d	–	–	–	4.35
57420		ch	31.49	1.76	4.19	4.3
57421		ch	29.44	1.58	4.14	4.57
57422		ch	31.13	1.54	3.4*	4.51
57423		ch	31.75	1.55	4.16	4.43
57424		ch	30.3	1.53	4.03	4.38
57425		d	–	–	–	3.39*
57426		ps	–	1.41	4.15	–
57427		ds	–	1.41	–	4.16
57428		ch	30.45	1.51	3.57	3.07*
57429	*Furipterus horrens*	d	–	–	–	2.63
57430	*Chrotopterus auritus*	ch	45.71	3.05	7.07	9.75

disarticulated bones in certain areas in the cave. Some coincide with the sites of accumulation of medium-sized mammals, while others are dispersed along the ducts of the cave system. The microvertebrate fauna thus preserved includes bats, rodents, and marsupials, as well as lizards and frogs. Regardless of how they entered the cave, many of the microvertebrates apparently were disarticulated and their bones transported after decomposition.

Two areas with concentrations of bones of small mammals were selected for sampling (fig. 3), and the one that was most intensively sampled was the site where a skeleton of †*Nothrotherium* sp. (Xenarthra, Nothrotheriidae) was found. The latter specimen represents the only source of age reference for these fossils thus far. At Beta Analytic Inc. (http://www.radiocarbon. com) significant amounts of collagen were successfully extracted from bone samples for AMS radiocarbon dating of the †*Nothrotherium* specimen, with a resulting date of 8700 ± 50 years BP (Perini et al., in prep.).

The *Nothrotherium* site covers an area of approximately 10 m² on the bottom of one of ducts that connects the main entrance of the Impossível cave, approximately 280 m from the entrance. A cross section of the so-called *Nothrotherium* duct is illustrated in figure 3 along with a sequence of photos that document the major passages of the duct. The *Nothrotherium*
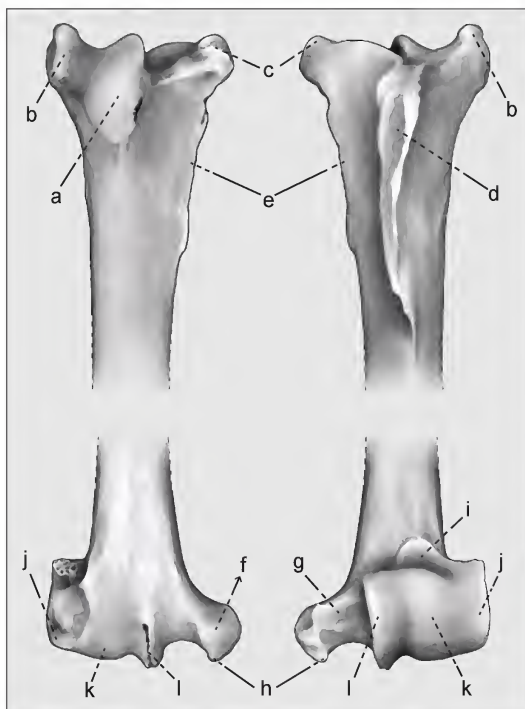

FIGURE 4. The terminology used to describe humerus morphology (modified from Czaplewski et al., 2008) with proximal ends at the top and distal ends at the bottom of the figure. Letters are indicated on a posterior view (left) and anterior view (right) of a left humerus of *Noctilio leporinus* (MN 47199): **a,** head; **b,** greater tuberosity (= trochiter); **c,** lesser tuberosity (= trochin); **d,** pectoral ridge; **e,** medial ridge; **f,** epitrochlea, the region located medial to the trochlea and including both the medial process and spinous process; **g,** medial process; **h,** spinous process; **i,** radial fossa; **j,** lateral ridge of capitulum; **k,** medial ridge of capitulum; **l,** trochlea.

site is oval in shape, submerged in a water column of approximately 8 m (depth apparently not significantly varying between dry and rainy seasons) with lateral walls separated by about 5 m. In one of the walls, laminar carbonate concretions are present at different depths, some close to the bottom level, which is covered by silt, clay, and sand grains. In order to collect microvertebrate remains associated with these submerged sediments, some of the established quadrants were collected by using a pressurized air-suction device or airlift (Salles et al., 1999). Sediments containing fossil fragments were sucked through a pipe that ended at a sequence of sieves of different square mesh sizes varying from 0.2 to 1.2 cm. A sequence of schematic illustrations (fig. 3A−C) shows how the airlift system was used at the Impossível-Ioiô cave system. Small samples of fossils were also collected by hand with the use of surgical gloves and

TABLE 2. Quaternary bat records from the Chapada Diamantina region compared with the extant records from the region and Quaternary records from elsewhere in the Neotropics.

Abbreviations and data sources as follows: **CD,** Chapada Diamantina Plateau, Bahia (Quaternary: Czaplewski and Cartelle, 1998; extant: Sbragia, 2012); **LS,** Lagoa Santa, Minas Gerais (Lund, 1840; Winge, 1892; Paula Couto, 1946); **SM,** Serra da Mesa, Goiás (Fracasso and Salles, 2005); **RRV,** Ribeira River Valley, São Paulo (Trajano and de Vivo, 1991; Ameghino, 1907); **Ga/Sa,** Garivaldino and Sangão sites, Rio Grande do Sul (Hadler et al., 2010); **Caa,** bat records from the Caatinga Biome that occurs in the Chapada Diamantina Plateau (Sá-Neto and Marinho-Filho, 2013); **SA,** South America, excepting Brazil (Morgan et al., 1988; Pardiñas and Tonni, 2000; Czaplewski et al., 2005); **CA,** Central America and Caribbean (Reynolds et al., 1953; Choate and Birney, 1968; Silva-Taboada, 1974, 1979; Olson et al., 1990; Arroyo-Cabrales and Polaco, 2008; Olson and Nieves-Rivera, 2010; Orihuela, 2012; Velazco et al., 2013); **NA,** North America (Mexico only) sites (Arroyo-Cabrales and Polaco, 2008); *, data from current work; **, first record for area.

	Brazil								SA	CA	NA
	Quaternary						Extant		Quaternary		
	CD	LS	SM	RV	Ga/Sa		CD	Caa			
FAMILY MORMOOPIDAE											
Mormoops megalophylla	+*								+	+	+
Pteronotus davyi	+		+					+			
Pteronotus gymnonotus	+**						+	+	+		
Pteronotus parnellii	+*		+					+	+	+	+
FAMILY NOCTILIONIDAE											
Noctilio leporinus	+**						+	+		+	
FAMILY PHYLLOSTOMIDAE											
Artibeus planirostris	+						+	+	+	+	+
Carollia perspicillata	+	+					+	+			
Chrotopterus auritus	+*	+	+	+	+		+	+	+		+
†Desmodus draculae	+			+					+	+	+
Desmodus rotundus	+	+	+				+	+	+	+	+
Diphylla ecaudata	+						+	+			
Lonchophylla mordax	+						+	+			
Mimon bennettii	+		+					+			
Phyllostomus discolor	+		+				+	+	+		
Phyllostomus hastatus	+	+	+				+	+	+		
Tonatia bidens	+	+						+			
FAMILY FURIPTERIDAE											
Furipterus horrens	+*							+			
FAMILY VESPERTILIONIDAE											
Eptesicus fuscus	+	+			+				+	+	+
FAMILY MOLOSSIDAE											
Eumops perotis	+	+						+	+		+
Molossus molossus	+				+		+	+		+	
Nyctinomops macrotis	+							+		+	
Promops nasutus	+	+									
Tadarida brasiliensis	+				+				+	+	+
TOTAL SPECIES	23	8	7	2	4		11	18	12	10	9

plastic zip bags. All remains representing the order Chiroptera were manually sorted from mixed packages of microvertebrate bones.

FIGURE 5. Posterior and anterior views of a distal portion of the right humerus of *Furipterus horrens* (MN 57429). Scale bar = 1mm.

SPECIMEN IDENTIFICATION

The fossils collected were deposited at the mammal section of the Museu Nacional–Universidade Federal do Rio de Janeiro. Identifications were based on literature descriptions and comparisons with extant specimens in the mammal collections of the Museu Nacional, Universidade Federal do Rio de Janeiro (MN); American Museum of Natural History, New York (AMNH); and Instituto Nacional de Antropología e Historia, México City (INAH) (appendix 1).

Standard measurements for the fossil humeri collected are presented in table 1. All specimens whose measurements are provided here were considered adults based on epiphyseal fusion. The terminology used for humerus morphology was standardized based on a modified version of that proposed by Czaplewski et al. (2008) (fig. 4). A comparative study of humeral morphology of *Noctilio* is provided in an attempt to reveal patterns of variation within the genus that could be used to identify fossils without relying exclusively on size.
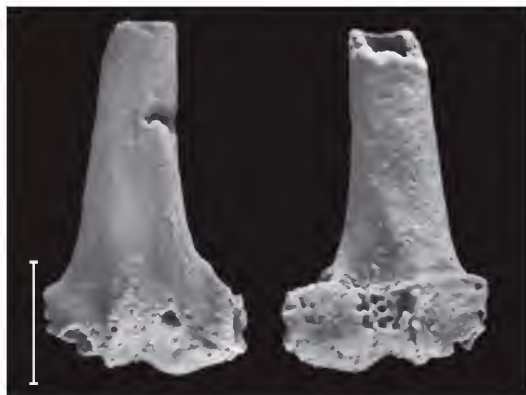
TAXONOMIC ACCOUNTS

A total of 33 humeral fragments of bats were recovered from the Impossível-Ioiô cave system. Six species from four families were identified based on this collection (table 2, appendix 2). Craniodental data will be addressed in a future publication. Taxonomic accounts for each family are provided below.

FAMILY FURIPTERIDAE GRAY, 1866

A distal end of a left humerus from Impossível-Ioiô is identified as *Furipterus horrens* (fig. 5), which represents the second fossil record for the species and the third for the family (Czaplewski and Cartelle, 1998; Morgan and Czaplewski, 1999). The first known fossil record of *F. horrens* (a left mandible and four humeri fragments) is also from the Quaternary of the Chapada Diamantina (Toca da Boa Vista; Czaplewski and Cartelle, 1998). The Chapada Diamantina records are consistent with the present distribution of the species, which ranges from Costa Rica to northeastern Brazil (Simmons, 2005; Peracchi et al., 2011), although it is considered a rare species and is difficult to collect with mist nets (Simmons and Voss, 1998; Bredt et al., 1999).

The humerus fragment from Impossível-Ioiô preserves only a small portion of the shaft with a damaged distal end. The dimensions of this specimen (table 1) fall well within the range

Furipterus horrens   *Natalus stramineus*
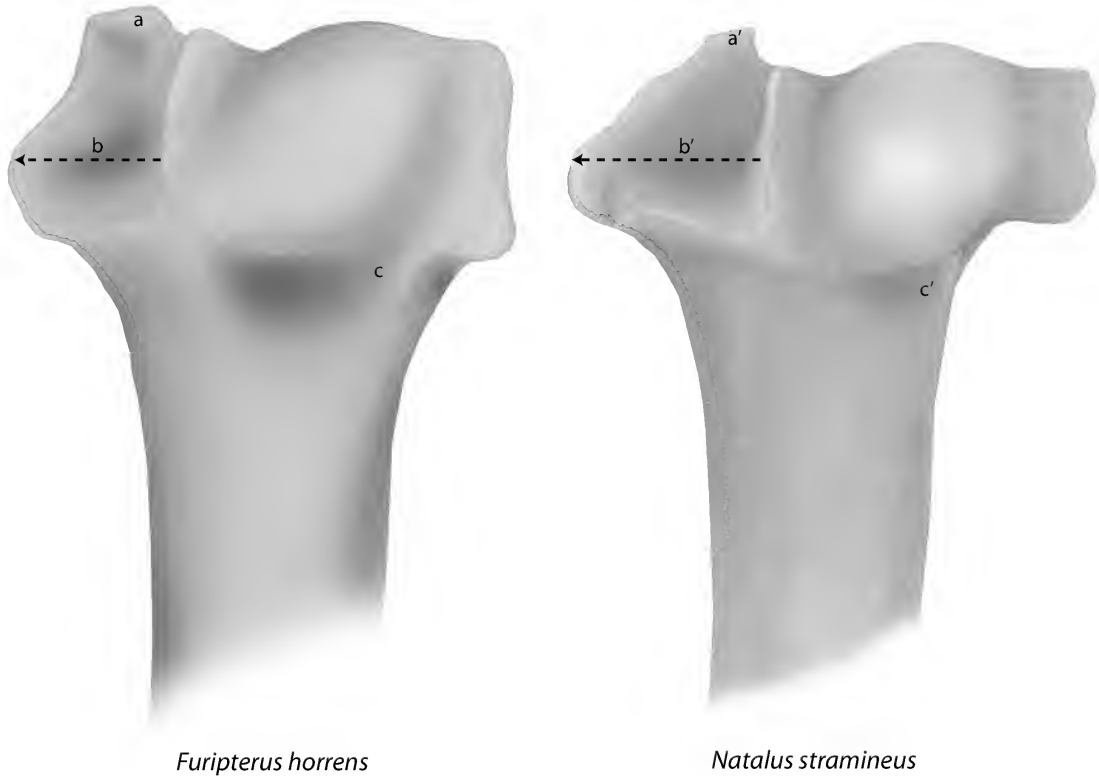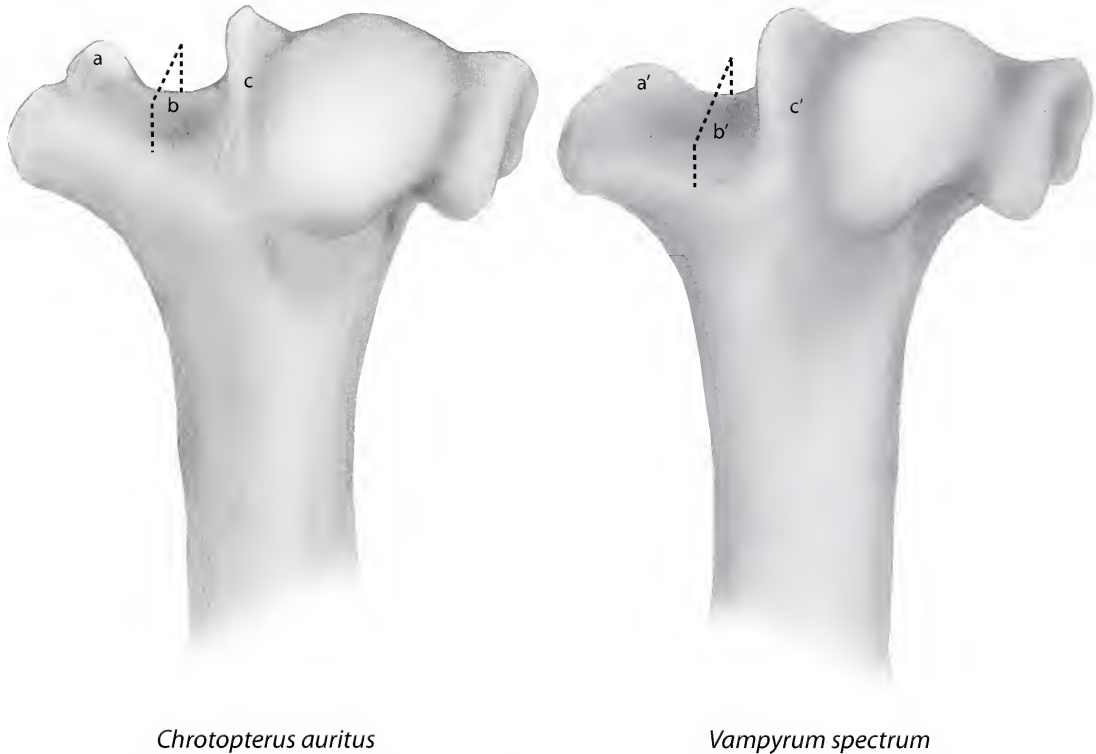
FIGURE 6. Differences in distal humeral morphology between *Furipterus horrens* (left) and *Natalus stramineus* (right) as seen in anterior view with lateral toward the right side of the figure; see text for discussion: (**a/a′**) shape and development of the spinous process (larger and more trapezoidal in *Furipterus*); (**b/b′**) development of the epitrochlea (less expanded mediolaterally in *Furipterus*); and (**c/c′**) development of the posterior surface of the lateral ridge of the capitulum (posterior surface expanded over the lateral border of a well-developed radial fossa in *Furipterus*).

of variation previously reported for *Furipterus horrens* (Czaplewski and Cartelle, 1998). Distal morphology of the humerus of *F. horrens* is distinct from that of other bats of comparable size, including thyropterids, natalids, emballonurids, and vespertilionids. The distal surface of the epitrochlea in *F. horrens* has a unique rounded and concave shape, with the anterolateral border extending over the anterior portion of the trochlea. The humerus in natalids such as *Natalus stramineus* resembles to a certain degree the general pattern found in *Furipterus*. However, *Furipterus* has a considerably larger and thicker trapezoidal spinous process, located directly adjacent to the posterior surface of the trochlea (fig. 6A), differing this way from natalids, but somewhat similar patterns are also observed among vespertilionids. This similarity in position with respect to the medial-lateral axis contrasts with significant differences in shape and direction of growth of the spinous process compared to that in vespertilionids, which display a markedly more posterior projection. The typical natalid medial extension of the posterior surface of the epitrochlea is entirely absent in *F. horrens* (b′ in fig. 6).

Extension of the posterior surface of the lateral ridge of the capitulum over the lateral border of a well-developed radial fossa (preserved in the fossil) is a character that unequivo-

Chrotopterus auritus

FIGURE 7. Anterior, posterior, lateral, and medial views of a right humerus of *Chrotopterus auritus* (MN 57430). Scale bar = 1mm.

cally distinguishes *Furipterus horrens* from both natalids (c/c′ in fig. 6) and thyropterids, although this condition is also present in other bat lineages, such as emballonurids and noctilionids. These two lineages, however, have a very different overall pattern of distal morphology, mostly in shape and degree of development of the trochlea and the spinous process, which is relatively elongated and detached from the trochlea in both families.

Chrotopterus auritus   *Vampyrum spectrum*

FIGURE 8. Differences in distal humeral morphology between *Chrotopterus auritus* (left) and *Vampyrum spectrum* (right) as seen in anterior view with lateral toward the right side of the figure; see text for discussion: (**a/a′**) shape and development of the spinous process (smaller and more trapezoidal in *Chrotopterus*); (**b/b′**) anteroposterior development (width) of the epitrochlea (narrower in *chrotopterus*); and (**c/c′**) degree of the development of the trochlea (narrower and less expanded over the epitrochlea in *Chrotopterus*).

FAMILY PHYLLOSTOMIDAE GRAY, 1825

The family Phyllostomidae is represented by humeral remains at Impossível-Ioiô by only one species, *Chrotopterus auritus* (fig. 7). The Pleistocene/Holocene records of this species are limited to reports from the Yucatán Peninsula of México (Arroyo-Cabrales and Alvarez, 1990), from Sierra de Perijá in Venezuela (Rincón, 1999), and from the following localities in Brazil: Lagoa Santa, Minas Gerais (Winge, 1892); Iporanga, São Paulo (Ameghino, 1907); Chapada Diamantina, Bahia (Cartelle and Abuhid, 1994; Czaplewski and Cartelle, 1998); Serra da Mesa, Goiás (Fracasso and Salles, 2005); and Brochier, Rio Grande do Sul (Hadler et al., 2010). These records include cranial and postcranial remains and are biogeographically consistent with the known extant distribution pattern of the species (Simmons, 2005).

The new record of *Chrotopterus auritus* from Chapada Diamantina consists of a single well-preserved right humerus that lacks only portions of the pectoral ridge and the tip of the spinous process (fig. 7). This specimen is the size and shape typical for the species. The shaft is arched with a concave curvature toward the middistal portion (viewed from the lateral side), and also exhibits torsion of this portion toward the medial side. This morphology also occurs in *Vampyrum spectrum* as well as in other phyllostomines such as *Trachops*

cirrhosus and *Tonatia saurophila.* The proximal end of the humerus in *Chrotopterus auritus* and *Vampyrum spectrum* are very similar. In both species the humerus has a nearly spherical humeral head and a lesser tuberosity that is either similar in size or a bit larger than the greater tuberosity (*Chrotopterus*) or a lesser tuberosity that is distinctly larger than the greater tuberosity (*Vampyrum*) (fig. 8). *Chrotopterus* has a humerus with a distal end that is slightly less robust than in *Vampyrum*, with a less well-developed radial fossa and an overall smaller epitrochlea. The epitrochlea has an elongated shape, narrowing toward the medial end with a somewhat triangular distal surface (associated with the median process), a condition shared by *Vampyrum* and other phyllostomids. Nevertheless, it is anteroposteriorly wider in *Vampyrum* compared to the condition observed in *Chrotopterus* (b/b′ in fig. 8). The spinous process in *Chrotopterus* is small, located near the medial end of the epitrochlea, and has a trapezoidal shape quite different from the lower and wider process seen in *Vampyrum* (a/a′ in fig. 8). The degree of development of the trochlea also distinguishes these two species, being considerably wider and expanded over the epitrochlea surface in *Vampyrum* (c/c′ in fig. 8). The sister-taxon relationship found between *Chrotopterus* and *Vampyrum* in recent phylogenies (Wetterer et al., 2000; Baker et al., 2003; Dávalos et al., 2012) seems unquestionably supported by the patterns of variation in the humerus morphology seen in the family Phyllostomidae.

FAMILY MORMOOPIDAE SAUSSURE, 1860

The family Mormoopidae is represented by a set of 27 humeral fragments identified as *Mormoops* cf. *megalophylla* (fig. 9), *Pteronotus gymnonotus* (fig. 11), and *P. parnellii* (fig. 12). The record of *Mormoops* is particularly noteworthy because these bats do not occur in the region today, instead having a distribution that is primarily limited to Central America and the Caribbean, with a very restricted range in northwestern South America (Simmons, 2005). The presence of the genus in the Quaternary of Chapada Diamantina was previously reported by Cartelle and coauthors (Cartelle and Abuhid, 1994; Czaplewski and Cartelle, 1998) based on craniodental remains as well as a number of humeri (although only measurements of a subset of 54 were provided). Those authors tentatively identified all of these fossils as *Mormoops megalophylla*, although they also suggested that, based on their large size, they might represent †*M. magna*, an extinct species exclusively known from humeri remains from Cuba and the Dominican Republic (Silva Taboada, 1974; Jiménez Vázquez et al., 2005; Velazco et al., 2013).

The new records of *Mormoops* recovered from the Impossível-Ioiô cave system consist of nine humeral fragments, four of which are complete and all of which we assign to *Mormoops* cf. *megalophylla.* These are unquestionably *Mormoops*, but biogeographic considerations and lack of comprehensive analyses of variation within the genus suggests that caution should be used in assigning them to *M. megalophylla.* The Chapada Diamantina fossils of *Mormoops* have a morphology very much like that of *M. megalophylla,* but they are slightly more robust than typical extant specimens, as pointed out by Czaplewski and Cartelle (1998). *M. megalophylla* differs from *M. blainvillei* in its significantly larger size (Silva Taboada, 1974; Rezsutek and Cameron, 1993). The morphology of the proximal

FIGURE 9. Anterior, posterior, medial, and lateral views of a left humerus of *Mormoops* cf. *megalophylla* (MN 57402). Scale bar = 1mm.

humerus is very similar in these taxa, but distally the species differ in the development of the trochlea with respect to its posterior extension over the anterior surface of the spinous process. In *M. megalophylla* this surface is relatively well developed, reaching the base of the spinous process at its most posterior extent. In contrast, *M. blainvillei* has the trochlea clearly less developed and ending at a more anterior plane (a/a′ in fig. 10). As can also be

Mormoops megalophylla   *Mormoops blaivillei*
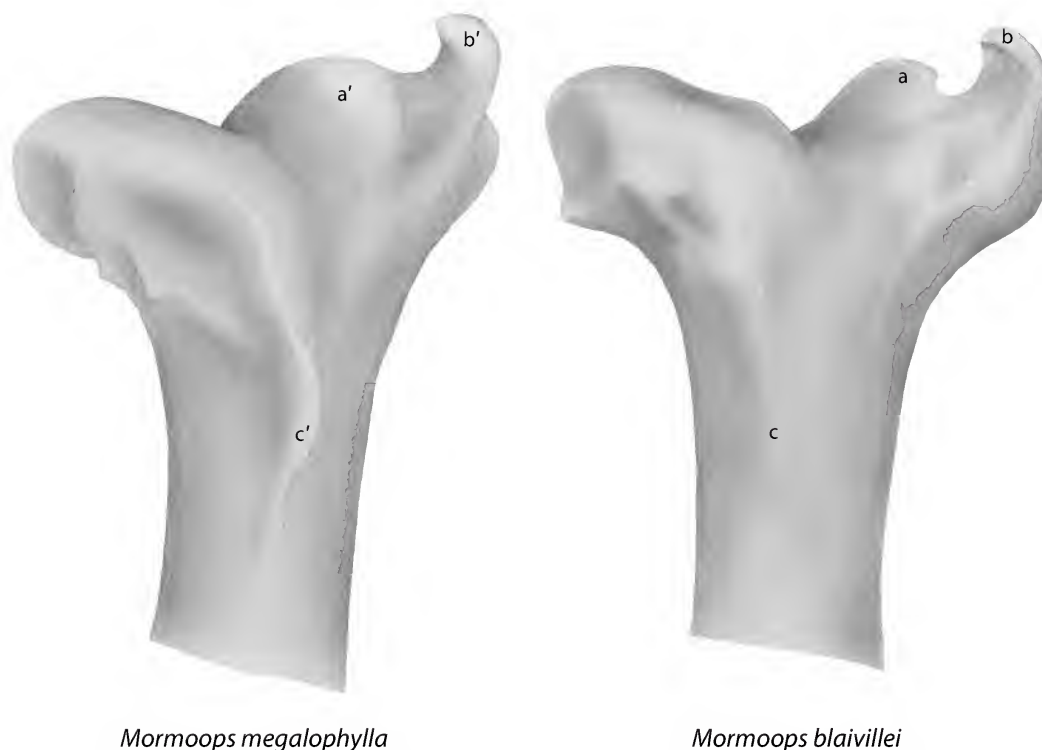
FIGURE 10. Differences in distal humeral morphology between *Mormoops megalophylla* (left) and *M. blainvillei* (right) as seen in posterior view with lateral toward the left side of the figure; see text for discussion: (**a/a′**) development and posterior extension of the trochlea (trochlea more strongly developed and extending further posteriorly in *M. megalophylla*); (**b/b′**) differences in shape and size of the spinous process (more bulbous distally and with strongly developed crestlike form posteriorly in *M. megalophylla*); and (**c/c′**) degrees of the development and shape of the posterolateral crest (more strongly developed in *M. megalophylla*).

seen in figure 10, the development and shape of the spinous process (b/b′) and of the posterolateral crest (c/c′) are distinct in these two species. The *Mormoops* samples from the Quaternary of Chapada Diamantina resemble *M. megalophylla* but have a slightly larger posterolateral crest (a structure on the posterior surface of the distal epiphysis extending over the shaft, laterally following the posterior ulna-trochlear facet) than that seen in our comparative sample of extant *Mormoops*. However, the significance of this trait, as well as the slight size differences observed, remain unclear. Accordingly, we treat the fossils of *Mormoops* from Chapada Diamantina as *M.* cf. *megalophylla*.

Pteronotus specimens are relatively abundant in the Chapada Diamantina collections, with 18 humeral fragments representing two species, *P. parnellii* and *P. gymnonotus.* Of the seven specimens representing *P. gymnonotus,* two are very well preserved, with one nearly intact and the other only slightly damaged proximally. Similarly, of the 11 humeri of *P. parnellii* in the collection, three are complete and three others have the shaft with both ends preserved but with some damage to various surfaces and processes. The morphology of the humerus in *Pteronotus* is quite different from that seen in *Mormoops*. The humerus of *Pteronotus* seemingly retains more of the basal

FIGURE 11. Anterior, posterior, lateral, and medial views of a right humerus of *Pteronotus gymnonotus* (MN 57413). Scale bar = 1mm.

noctilionoid morphology, mostly notably in the distal end. The main diagnostic features that distinguish the genus *Pteronotus* from other noctilionoids include the prominent anterior position of the humeral head relative to the greater tuberosity (the latter structure being more posteriorly positioned in *Pteronotus* than in other noctilionoids), and the marked posterolateral displacement of the spinal process, which is partially dissociated from the medial process.

FIGURE 12. Anterior, posterior, medial, and lateral views of a left humerus of *Pteronotus parnellii* (MN 57423). Scale bar = 1mm.

Within *Pteronotus* a number of features of both the proximal and distal ends of the humerus allow unequivocal species identifications, with the distal end more drastically modified. Differences among species include variation in shape, angle, and degree of development of the lesser tuberosity at the proximal end, and at the distal end variation in trochlear shape, position, size, and in the relationship between the trochlea and the spinous process. The

humeri of *P. parnellii* and *P. gymnonotus* stand clearly as the two largest in the genus, with *P. parnellii* the larger. Similar size distinctions are also observed among the fossils, although they are overall somewhat smaller than the extant specimens examined (a topic to be addressed further in future contributions). The morphology of the proximal end of the humerus of *P. parnellii* differs from that of *P. gymnonotus* in a number of details. The most conspicuous difference involves the development of the midbasal portion of the anterior surface of the greater tuberosity, which is wider in *P. gymnonotus*, extending over the anterior extremity of the supraglenoid fossa (a somewhat similar condition is also observed in *P. macleayii* and *P. quadridens*, and to a certain extent also in *P. personatus* and *P. davyi*). In contrast, in *P. parnellii* the basal portion of the greater tuberosity is relatively narrow and the anterior extremity of the supraglenoid fossa is more open, a condition shared by other noctilionoids. The most obvious distinction between the distal ends of the humeri of *Pteronotus parnellii* and *P. gymnonotus* concerns the position and angle of development of the spinous process. *Pteronotus parnellii* exhibits a unique condition in which the spinous process is located near a midline between the anterior and posterior plane of the shaft and projects distally, whereas in *P. gymnonotus* the spinous process is placed much more posteriorly from that midline, projecting more posteriorly and with its tip extending over the limits of the posterior surface of the shaft (a/a′ in fig. 13). The latter condition is shared by all species of *Pteronotus* (including the extinct species †*P. pristinus*) except for *P. parnellii*. *Pteronotus* species are also distinguished by different shapes of the distal trochlea when seen in lateral view, with this flange in *P. parnellii* displaying a circular outline as opposed to a more rectangular outline in *P. gymnonotus* (b/b′ in fig. 13). The fossils of the two species from Chapada Diamantina have a distal humeral morphology that conforms well to the known patterns of *P. parnellii* and *P. gymnonotus* as described above.

Pteronotus gymnonotus was documented as an extant taxon from Chapada Diamantina (Sbragia, 2012), but fossils of this species have not been previously reported from the region (Cartelle and Abuhid, 1994; Czaplewski and Cartelle, 1998). This species is known from the fossil record of South America only from a single locality, Cueva Toromo, Venezuela (Rincón, 1999). Material identified as *Pteronotus* aff. *gymnonotus* by Cartelle and Abuhid (1994) was reexamined by Czaplewski and Cartelle (1998), who reidentified it as *P. parnellii*, a species not known from the extant fauna of the Chapada Diamantina.

FAMILY NOCTILIONIDAE GRAY, 1821

The evolutionary history of the bulldog bats (genus *Noctilio*) extends at least to the late Tertiary of South America. A series of upper and lower molars nearly indistinguishable from those of modern *Noctilio* were reported by Czaplewski (1997) and Czaplewski et al. (2003) from the Middle Miocene (11.8–12.5 mya) of La Venta, Colombia. Based on size and morphology, these authors identified the La Venta fossils as *Noctilio albiventris*. Another fragmentary *Noctilio* fossil from the Miocene—a lower m1 from Rio Acre, 30 km W of Iñapari, Department of Madre de Dios, Peru—dates to the Huayquerian South American Land Mammal Age (9.5 mya). Because this specimen does not appear to fit within the range of variation known for *N. albiventris*,

Czaplewski (1996) named it as a new species, †*N. lacrimaelunaris*. Merino et al. (2007) described an upper incisor referable to *Noctilio* sp. from deposits dated approximately 0.4 mya (Middle Pleistocene) from Las Grutas, Necochea, Province of Buenos Aires, Argentina. This discovery extended the known range for the genus at least 6° S latitude from the present distribution. However, the highly incomplete nature of the specimen precluded identification to species level.

Fossils assigned to the larger species of *Noctilio, N. leporinus,* have been found in Late Pleistocene and Holocene cave deposits of Barbuda, Cuba, and Puerto Rico (Reynolds et al., 1953; Choate and Birney, 1968; Silva Taboada, 1979; Pregill et al., 1994). However, no such fossils have been previously reported from mainland sites despite the fact that the species today ranges from Sinaloa, Mexico, south through Central and South America as far as northern Argentina and Paraguay (Simmons, 2005; Gardner, 2008a). New remains of *Noctilio* recovered from Chapada Diamantina stand as the first confirmed Quaternary record of the species *N. leporinus* (fig. 14) for South America. The material consists of two well-preserved humeral fragments and a few craniodental remains (the latter to be described in a subsequent publication). *Noctilio leporinus* has been reported from the extant fauna of the Chapada Diamantina (Oliveira and Pessôa, 2005), although no voucher specimen is known.

The morphology of the humerus of *Noctilio* is quite distinctive from that seen in other noctilionoids. The shaft is nearly straight and both proximal and distal articular surfaces lie in line with the shaft (fig. 14). Proximally, the humerus has an elliptical head, a feature not observed in any other noctilionoid except *Mormoops*. Distally, the humerus exhibits a unique medially extended epitrochlea, with the spinous process placed at its extremity.

The most obvious difference in humeral morphology between *Noctilio leporinus* and *N. albiventris* concerns size, with the humerus of *N. leporinus* much larger and more robust than that of *N. albiventris*. The cross-sectional shape of the shaft near the distal epiphysis also varies between these taxa: in *N. albiventris* the shaft tends to be more cylindrical in cross section, as opposed to a more rectangular cross-sectional shape in *N. leporinus* (c/c′ in fig. 15). Proximally, *N. albiventris* has a humeral head with a constriction toward the anterior end (associated with a prominent laterally curved proximal edge), which contrasts with a more smoothly rounded condition observed in *N. leporinus*. Distally, among some specimens of *N. albiventris*, the proximal border of the radial fossa has a prominent curved form (apparently correlated with the shaft having a cylindrical cross section near the epiphysis). This contrasts with the condition of *N. leporinus* in which the proximal border of the radial fossa is not as well developed over the anterior surface of the shaft (b′ in fig. 15). The epitrochlea is proportionally somewhat more mediolaterally expanded in *N. leporinus* than in *N. albiventris*. *Noctilio leporinus* has a distinct medial process that projects slightly over the anterior border of the epitrochlea, whereas this process is not developed in *N. albiventris* (e/e′ in fig. 15). The spinous process in *N. leporinus* has a relatively conspicuous tip that is recurved laterally and somewhat posteriorly oriented, whereas in *N. albiventris* the spinous process is relatively poorly developed, not recurved, and is partially fused with the lateral end of the epitrochlea (f/f′ in fig. 15). In *N. leporinus* the anteroproximal rim of the lateral ridge of the capitulum is narrow and forms a pointed tip that is curved toward the posterior

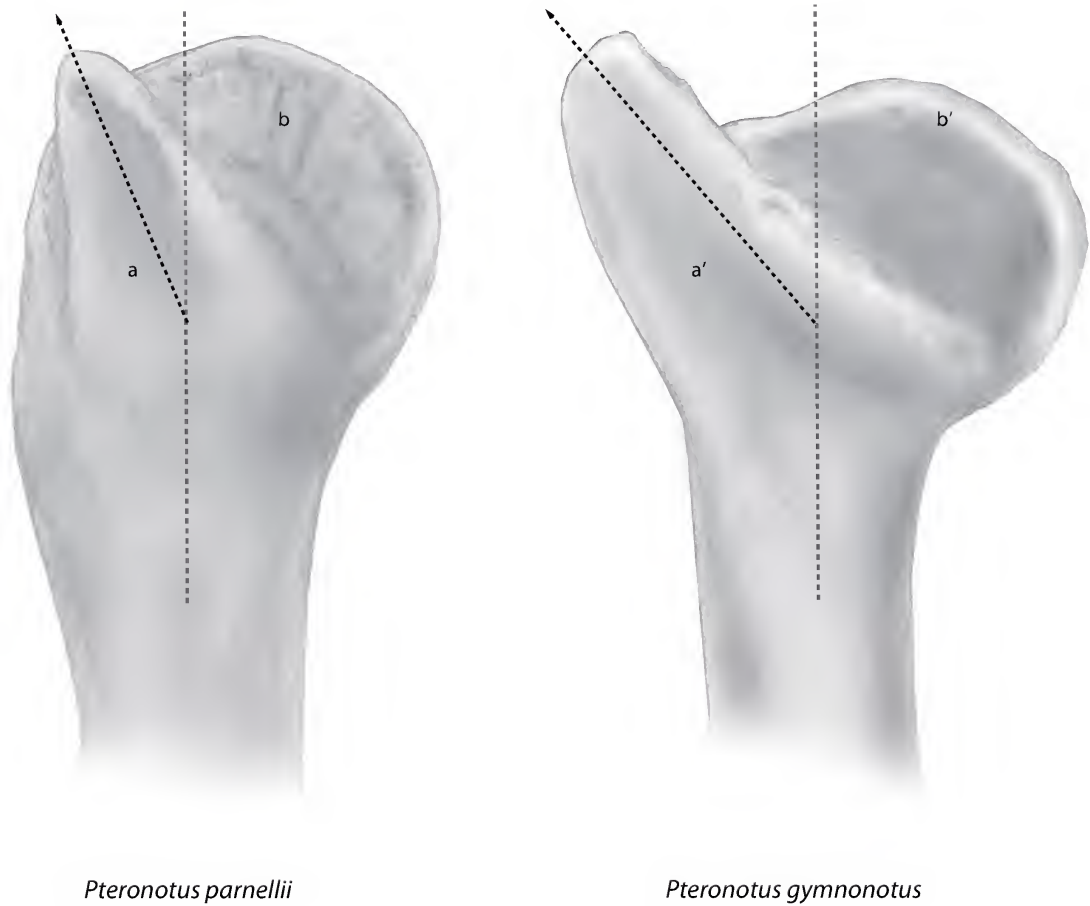Pteronotus parnellii   Pteronotus gymnonotus

FIGURE 13. Differences in distal humerus morphology between *Pteronotus parnellii* (left) and *P. gymnonotus* (right) as seen in medial view with posterior toward the left of the figure; see text for discussion: (**a/a'**) differences in degree of development and orientation of the epitrochlea and spinous process (epitrochlea less developed and spinous process shorter and directed more distally in *P. parnellii*); and (**b/b'**) differences in the outline of the trochlea (more circular in medial view in *P. parnellii*).

side, whereas in *N. albiventris* this process is more rounded (a/a' in fig. 15). The *Noctilio* humerus fossils from Chapada Diamantina are clearly referable to *N. leporinus* based on both size and morphology.

The genus *Noctilio* is in need of review and patterns of morphological variation within species need to be reevaluated with larger sample sizes from more localities to better control for intraspecific variation. Phylogeographic studies of Lewis-Oritt et al. (2001) and Pavan et al. (2013) have suggested that *N. albiventris* as currently recognized is composed by more than one taxon (see below). However, there is no evidence that *N. leporinus* represents of more than one species despite its broad geographic distribution (Lewis-Oritt et al., 2001; Pavan et al., 2013).

DISCUSSION AND CONCLUSIONS

The Caatinga biome, one of two biomes entirely contained within the country of Brazil, is situated between a narrow strip of the Atlantic Rainforest biome, the eastern extent of the Cerrado biome, and the easternmost extent of the Amazonian biome (Leal et al., 2003; Prado, 2003). Despite its key location, little is known about the fauna of the Caatinga in comparison with the more heavily studied biogeographic regions that surround it (Leal et al., 2003). The Caatinga is usually described as a semiarid biome with intermittent rains and periodic severe drought seasons, and it harbors a mosaic of xerophytic and semiarid-adapted vegetation (Prado, 2003; Ab'Sáber, 2007). However, what is usually called "Caatinga" is actually composed of a multitude of vegetation profiles, including open savannas, dry forests, and rocky outcrops (Prado, 2003). The Caatinga has been traditionally considered to be relatively low in endemism when compared to other Brazilian biomes, but recent studies have shown that it has more endemic species than previously suspected (Prado, 2003; Leal et al., 2005). Given the general lack of knowledge, the number of species inhabiting the Caatinga is potentially very high since most of the region has never been surveyed (Leal et al., 2005). For mammals alone, at least 143 species are known for the Caatinga region, with two endemic rodent species (Oliveira et al., 2003). Recently described endemic bat species (Gregorin and Ditchfield, 2005) testify that the actual mammal diversity of the Caatinga biome may be underestimated, especially in the case of bats. Knowing the true extent of the diversity of Caatinga mammals is of importance for understanding the biogeographic dynamics of the region, especially given its pivotal position and contact zones with three other biomes (Amazonia, Atlantic Rainforest, and Cerrado). Understanding the dynamics of contraction and expansion of the mesic regions of Amazonia and Atlantic Rainforest during the Pleistocene will require knowledge of both modern and past faunas of the region (Prado, 2003; Santos et al., 2007).

The bat fauna currently known from the Caatinga biome consists of 86 extant species of bats (Sá-Neto and Marinho-Filho, 2013). Of those, at least 22 are currently known for the Chapada Diamantina plateau, the number being perhaps as high as 24 (Oliveira and Pessôa, 2005; Sbragia, 2012). The Chapada Diamantina is not a homogeneous environment, instead consisting of a mosaic of different kinds of vegetation including dry and riparian forests, rocky outcrops, and enclaves of Cerrado vegetation (Rocha et al., 2005). Bat distributions are likely influenced by this heterogeneity, although studies suggest that most species of bats are widely distributed along different environments (Oliveira and Pessôa, 2005; Sá-Neto and Marinho-Filho, 2013). The Chapada Diamantina is also extremely rich in caves, a factor that may have a great influence on the occurrence of bats since roost availability may be a limiting factor in open environments (Aguirre, 2002). Gregorin and Mendes (1999) found 11 species of bats in a single cave of the Chapada Diamantina, about half of the diversity known for the entire region.

One of the challenges of documenting the diversity of fossil bats for comparison to living communities is the incomplete nature of available specimens. The current study documents the value of humeral morphology for faunal and taxonomic analyses of bat paleofaunas, particularly those preserved in caves. Fossil bat assemblages in caves often consist largely of limb bones, with the humerus typically well represented (Czaplewski and Cartelle, 1998; Czaplewski

FIGURE 14. Anterior, posterior, medial, and lateral views of a left humerus of *Noctilio leporinus* (MN 57400). Scale bar = 1mm.

et al., 2005; Grady and Olson, 2006). Humeral remains are frequently well preserved, probably because this bone in bats is robust and highly mineralized in comparison with other wing elements (Swartz et al., 2012). Although humeri have been used to identify bat species in many previous studies (e.g., Czaplewski et al., 2005; Grady and Olson, 2006), detailed descriptions of specific diagnostic features of the humerus are lacking for most extant taxa. Recently

Noctilio leporinus   *Noctilio albiventris*
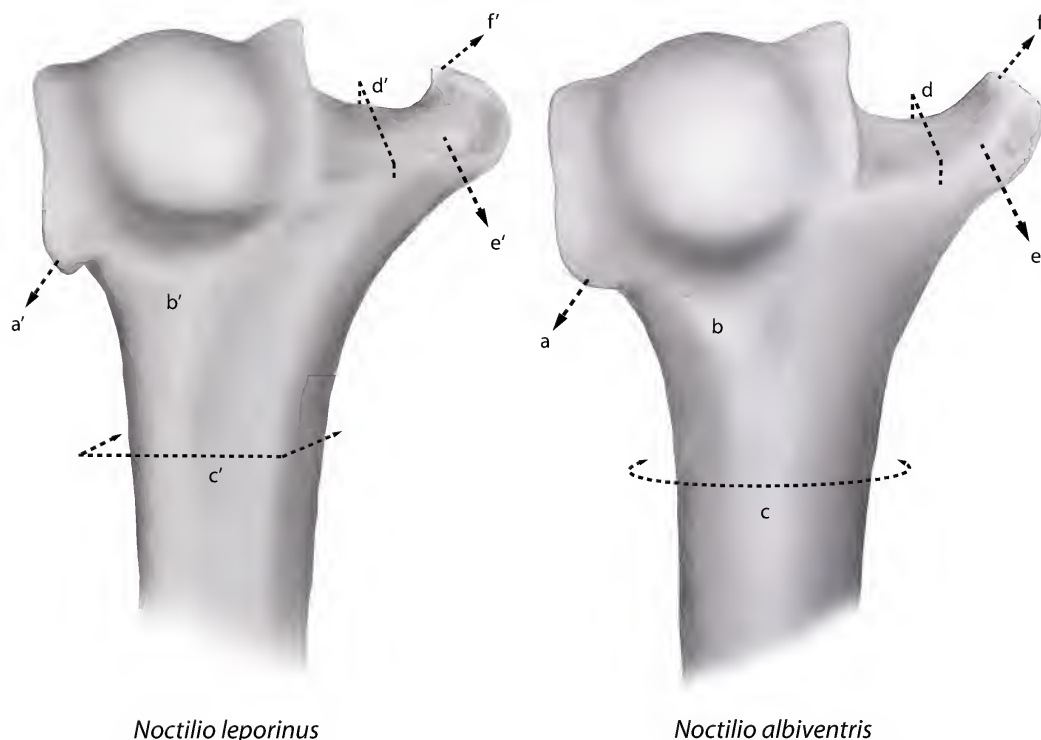
FIGURE 15. Differences in distal humerus morphology between *Noctilio leporinus* (left) *N. albiventris* (right) and as seen in anterior view with lateral toward the left side of the figure; see text for discussion: (**a/a′**) shape of anteroproximal portion of the lateral ridge of the capitulum (narrower and forming a pointed tip in *N. leporinus*); (**b/b′**) development of the proximal border of the radial fossa (border poorly defined in *N. leporinus*); (**c/c′**) cross-sectional shape of the shaft near its distal end (more rectangular in *N. leporinus);* (**d/d′**) anteroposterior width of the epitrochlea (wider in *N. leporinus*); (**e/e′**) degree of development of the medial process (more distinct and projecting slightly over the anterior border of the epitrochlea in *N. leporinus*); (**f/f′**) development and position of the spinous process (better developed and with a laterally recurved tip in *N. leporinus*).

Czaplewski and Morgan (2012) described 20 morphological characters of the humerus potentially useful for phylogenetic studies of noctilionoids, and we plan to build upon these in future projects. Ongoing studies comparing humeri from species across all bat families confirm a high degree of species-specific morphological variation in this wing element (Salles et al., in prep.).

With the additional records reported here, the Quaternary bat fauna of Chapada Diamantina is the second most diverse locality known from the Quaternary of Brazil, with 29 bat species representing eight families and 24 genera. The Quaternary bat fauna of Chapada Diamantina includes the extinct giant vampire †*Desmodus draculae* as well as the genus *Mormoops*, which is not known from extant faunas in southern South America. Another 11 records (table 2) are not known from the extant fauna of the Chapada Diamantina plateau, although extant representatives of these species have been recorded from other localities in the Caatinga or Atlantic forest (Gardner, 2008b; Sá-Neto and Marinho-Filho, 2013). Most of the latter species belong to the families Mormoopidae and Molossidae, known for being difficult to capture using

standard collecting methods (e.g., ground-level mist nets; Voss and Emmons, 1996; Simmons and Voss, 1998). We expect that future surveys using other methods (e.g., harp traps, roost searching, canopy netting, echolocation call surveys) may find that these taxa are indeed present in the extant fauna of the Chapada Diamantina plateau.

Records from the fossil fauna of Chapada Diamantina are potentially noteworthy from the perspective of historical biogeography. The *Mormoops* cf. *megalophylla* records reported here and by Czaplewski and Cartelle (1998) represent a significant range extension for the genus, whose current distribution extends only as far south as Colombia and Venezuela (Simmons, 2005). Extant populations from northern South America are recognized as a distinct subspecies, *M. megalophylla tumidiceps,* which is thought to be the sister group to Central/North American lineages (Dávalos, 2006). The Caribbean species, *M. blainvillei*, is in turn the sister group to this clade (Dávalos, 2006). It is not yet clear where the Chapada Diamantina *Mormoops* fits relative to these taxa, but it could be informative about the origins and diversification of the *M. megalophylla* lineage. In addition to biogeography, the record of *Mormoops* from Chapada Diamantina is also noteworthy because, based on the only age reference currently available for this fossil assemblage, it could be more than 10,000 years younger than the previous record (Czaplewski and Cartelle, 1998), suggesting that the genus remained a part of the Brazilian bat fauna until relatively recently. Future extractions of collagen from bone samples may shed light on the accurate age of the fossil bats from Chapada Diamantina. Regardless of whether the Chapada Diamantina *Mormoops* represents *M. megalophylla* or a similar undescribed species, inclusion of this taxon in future phylogenies and biogeographic analyses may shed light on the evolutionary history of the genus and correlations of mormoopid evolution with paleoenvironmental fluctuations during the late Pleistocene–Holocene.

Our understanding of the evolutionary history of the genus *Noctilio* is also enhanced by the Chapada Diamantina fossils. Fossils have previously provided a tantalizing yet highly limited view of early noctilionid evolution. The existence of bats apparently morphologically indistinguishable from modern *N. albiventris* in the Miocene might be interpreted as indicative of relative stasis in evolution of this group over a long period (~12 mya). In principle at least, this morphospace—for a medium-sized *Noctilio* (20–45 g)—has been around for more than 10 million years. However, the La Venta Miocene fossils consist of only a few isolated teeth (Czaplewski, 1997). In this context it is noteworthy that recent molecular phylogenetic studies have questioned the monophyly of extant bats referred to *N. albiventris*, suggesting that *albiventris* as currently recognized may represent a complex of at least three species that together are paraphyletic with respect to *N. leporinus* (Lewis-Oritt et al., 2001; Pavan et al., 2013). Pavan et al. (2013) found that living lineages of *Noctilio albiventris* originated quite recently, between 1.2–3.4 mya. The later finding is consistent with the idea that the La Venta fossils referred to *N. albiventris* probably represent a morphologically similar yet distinct species, and should not be assumed to indicate that *N. albiventris* is some sort of living fossil.

Based on a phylogenetic analysis including both mitochondrial and nuclear genes, Lewis-Oritt et al. (2001) hypothesized that *N. leporinus* quite recently diverged from within the *N.*

albiventris complex, roughly 0.28–0.7 mya. Recently, Pavan et al. (2013) conducted a new phylogeographic analysis for the genus and proposed that *N. leporinus* differentiated a bit earlier than suggested by Lewis-Oritt et al. (2001), with date estimates ranging between 0.8–1.3 mya. Pavan et al. (2013) found support for a sister-group relationship between an Amazonian clade of *N. albiventris* and *N. leporinus*. However, phylogeographic analyses within the latter taxon suggest that *N. leporinus* arose in the Caribbean region and only later colonized South America. Three extant subspecies of *N. leporinus* have traditionally been recognized: *N. l. mastivus* (Caribbean islands and México south to northern Ecuador, Colombia, and Venezuela), *N. l. leporinus* (Guianas and the Amazon lowlands of Colombia, Ecuador, Peru, and northeastern Brazil), and *N. l. rufescens* (eastern Bolivia, Paraguay, northern Argentina, and southeastern Brazil) (Hood and Jones, 1984; Simmons, 2005). Pavan et al. (2013) found only partial correlation between their genetic results and these taxa as defined above, with *N. l. mastivus* from the Caribbean and México appearing as a paraphyletic assemblage relative to a South American clade of *N. leporinus*. No clear support for *N. l. rufescens* as a distinct lineage was found. Coalescent analyses suggested that the South American clade originated only 176,000 years BP and underwent rapid demographic expansion. The discovery of fossils of *N. leporinus* at Chapada Diamantina indicates that this species was already present in eastern Brazil by the late Quaternary, consistent with the idea of a rapid, successful expansion of *N. leporinus* across the continent.

REFERENCES

Ab'Sáber, A. 2007. Os domínios da natureza no Brasil: potencialidades paisagísticas. Cotia: Ateliê Editorial.

Aguirre, L.F. 2002. Structure of a Neotropical savanna bat community. Journal of Mammalogy 83: 775–784.

Ameghino, F. 1907. Notas sobre una pequeña colección de huesos de mamíferos procedentes de las grutas calcarías de Iporanga, en el Estado de São Paulo, Brazil. Revista do Museu Paulista 7: 59–124.

Arroyo-Cabrales, J., and T. Alvarez. 1990. Restos óseos de murciélagos: procedentes de las excavaciones en las grutas de Lóltun. Colección Científica, Instituto Nacional de Antropología e Historia, México 194: 1–103.

Arroyo-Cabrales, J., and O.J. Polaco. 2008. Fossil bats from Mesoamerica. Arquivos do Museu Nacional 66: 155–160.

Auler, A., and A.R. Farrant. 1996. A brief introduction to karst and caves in Brazil. Proceedings of the University of Bristol Spelaeological Society 20: 187–200.

Baker, R.J., C.A. Porter, S.R. Hoofer, and R.A. van den Bussche. 2003. A new higher-level classification of New World leaf-nosed bats based on nuclear and mitochondrial DNA sequences. Occasional Papers of the Museum of Texas Tech University 230: 1–32.

Bredt, A., W. Uieda, and E.D. Magalhães. 1999. Cave bats from the Distrito Federal area in mid-western Brazil (Mammalia, Chiroptera). Revista Brasileira de Zoologia 16: 731–770.

Cartelle, C., and V.S. Abuhid. 1994. Chiroptera do Pleistoceno final – Holoceno da Bahia. Acta Geologica Leopoldensia 18: 429–440.

Choate, J.R., and E.C. Birney. 1968. Sub-Recent Insectivora and Chiroptera from Puerto Rico, with the description of a new bat of the genus *Stenoderma*. Journal of Mammalogy 49: 400–412.

da Cruz, F.W., Jr. 1998. Aspectos geomorfológicos e geoespeleologia do carste da região de Iraquara, centro norte da Chapada Diamantina, Estado da Bahia. Master's thesis, Instituto de Geociências, Universidade de São Paulo. 108 pp.

Czaplewski, N.J. 1996. Opossums (Didelphidae) and bats (Noctilionidae and Molossidae) from the late Miocene of the Amazon basin. Journal of Mammalogy 77: 84–94.

Czaplewski, N.J. 1997. Chiroptera. *In* R.F. Kay, R.H. Madden, R.L. Cifelli, and J.J. Flynn (editors), Vertebrate paleontology in the Neotropics: the Miocene fauna of La Venta, Colombia: 410–431. Washington, DC: Smithsonian Institution Press.

Czaplewski, N.J., and C. Cartelle. 1998. Pleistocene bats from cave deposits in Bahia, Brazil. Journal of Mammalogy 79: 784–803.

Czaplewski, N.J., and G.S. Morgan. 2012. New basal noctilionioid bats (Mammalia: Chiroptera) from the Oligocene of subtropical North America. *In* G.F. Gunnell and N.B. Simmons (editors), Evolutionary history of bats: fossils, molecules, and morphology: 317–352. Cambridge: Cambridge University Press.

Czaplewski, N.J., M. Takai, T.M. Naeher, N. Shigehara, and T. Setoguchi. 2003. Additional bats from the middle Miocene La Venta fauna of Colombia. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 27: 263–282.

Czaplewski, N.J., A.D. Rincón, and G.S. Morgan. 2005. Fossil bats (Mammalia: Chiroptera) remains from Inciarte Tar Pit, Sierra de Perijá, Venezuela. Caribbean Journal of Science 41: 768–781.

Czaplewski, N.J., G.S. Morgan, and S.A. McLeod. 2008. Chiroptera. *In* C.M. Janis, G.F. Gunnell, and M.D. Uhen (editors), Evolution of Tertiary mammals of North America: 174–197. Cambridge: Cambridge University Press.

Dávalos, L.M. 2006. The geography of diversification in the mormoopids (Chiroptera: Mormoopidae). Biological Journal of the Linnean Society 88: 101–118.

Dávalos, L.M., A.L. Cirranello, J.H. Geisler, and N.B. Simmons. 2012. Understanding phylogenetic incongruence: lessons from phyllostomid bats. Biological Reviews 87: 991–1024.

Fracasso, M.P., and L.O. Salles. 2005. Diversity of Quaternary bats from Serra da Mesa (State of Goiás, Brazil). Zootaxa 817: 1–19.

Gardner, A.L. 2008a [2007]. Family Noctilionidae Gray, 1821. *In* A.L. Gardner (editor), Mammals of South America. Marsupials, xenarthrans, shrews, and bats: 384–389. Chicago: University of Chicago Press.

Gardner, A.L. (editor) 2008b [2007]. Mammals of South America. Marsupials, xenarthrans, shrews, and bats. Chicago: University of Chicago Press.

Grady, F.V., and S.L. Olson. 2006. Fossil bats from Quaternary deposits on Bermuda (Chiroptera: Vespertilionidae). Journal of Mammalogy 87: 148–152.

Gregorin, R., and L.F. Mendes. 1999. Sobre quirópteros (Emballonuridae, Phyllostomidae, Natalidae) de duas cavernas da Chapada Diamantina, Bahia, Brasil. Iheringia, Série Zoologia 86: 121–124.

Gregorin, R., and A.D. Ditchfield. 2005. New genus and species of nectar-feeding bat in the tribe Lonchophyllini (Phyllostomidae: Glossophaginae) from northeastern Brazil. Journal of Mammalogy 86: 403–414.

Hadler, P., J. Ferigolo, and A.M. Ribeiro. 2010. Chiroptera (Mammalia) from the Holocene of Rio Grande do Sul State, Brazil. Acta Chiropterologica 12: 19–27.

Hood, C.S., and J.K. Jones, 1984. *Noctilio leporinus*. Mammalian Species 216: 1–7.

Hubbe, A., et al. 2011. Identification and importance of critical depositional gaps in pitfall cave environments: The fossiliferous deposit of Cuvieri Cave, eastern Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 312: 66–78.

Jiménez Vázquez, O., M.M. Condis, and E. García Cancio. 2005. Vertebrados post-glaciales en un residuario *fósil de Tyto alba scopoli* (Aves: Tytonidae) en el occidente de Cuba. Revista Mexicana de Mastozoología 9: 85–112.

Laureano, F.V. 1998. O registro sedimentar clástico associado aos sistemas de cavernas Lapa Doce e Torrinha, município de Iraquara, Chapada Diamantina, BA. Master's thesis, Instituto de Geociências, Universidade de São Paulo. 99 pp.

Laureano, F.V., and F.W. da Cruz Jr. 2002. Grutas de Iraquara (Iraquara, Seabra e Palmeiras), BA. *In* C. Schobbenhaus, D.A. Campos, E.T. Queiroz, M. Winge, and M.L.C. Berbert-Born (editors), Sítios geológicos e paleontológicos do Brasil, 1st ed.: 461–468. Brasília: Comissão Brasileira de Sítios Geológicos e Paleobiológicos (SIGEP).

Leal, I.R., M. Tabarelli, and J.M.C. Silva (editors). 2003. Ecologia e conservação da Caatinga. Recife: Editora Universitária – UFPE.

Leal, I.R., J.M.C. Silva, M. Yabarelli, and T.E. Lacher, Jr. 2005. Changing the course of biodiversity conservation in the Caatinga of northeastern Brazil. Conservation Biology 19: 701–706.

Lewis-Oritt, N., R.A. van den Bussche, and R.J. Baker. 2001. Molecular evidence for evolution of piscivory in *Noctilio* (Chiroptera: Noctilionidae). Journal of Mammalogy 82: 748–759.

Lund P.W. 1840. Nouvelles recherches sur la faune fossile du Brésil (extraits d'une lettre adressée aux rédacteurs, et datée de Lagoa Santa, 1er avril 1840). Annales des Sciences Naturelles, Zoologie 13: 310–319.

Merino, M.L., M.A. Lutz, D.H. Verzi, and E.P. Tonni. 2007. The fishing bat *Noctilio* (Mammalia, Chiroptera) in the Middle Pleistocene of central Argentina. Acta Chiropterologica 9: 401–407.

Morgan, G.S., O.G. Linares, and C.E. Ray. 1988. New species of fossil vampire bats (Mammalia, Chiroptera, Desmodontidae) from Florida and Venezuela. Proceedings of the Biological Society of Washington 101: 912–928.

Morgan, G.S., and N.J. Czaplewski. 1999. First fossil record of *Amorphochilus schnablii* (Chiroptera: Furipteridae), from the late Quaternary of Peru. Acta Chiropterologica 1: 75–79.

Oliveira, J.A., and L.M. Pessôa. 2005. Mamíferos. *In* F.A. Juncá, L. Funch, and W. Rocha (editors), Biodiversidade e conservação da Chapada Diamantina: 377–405. Brasília: Ministério do Meio Ambiente.

Oliveira, J.A., P.R. Gonçalves, and C.R. Bonvicino. 2003. Mamíferos da Caatinga. *In* I.R. Leal, M. Tabarelli, and J.M.C. Silva (editors), Ecologia e conservação da caatinga: 275–302. Recife: Editora Universitária – UFPE.

Olson, S.L., and A.M. Nieves-Rivera. 2010. Evidencia fósil y probable extinción del murciélago pescador *Noctilio leporinus* (Chiroptera: Noctilionidae) en Isla de Mona, Puerto Rico. Mastozoología Neotropical 17: 167–170.

Olson, S.L., G.K. Pregill, and W.B. Hilgartner. 1990. Studies on fossil and extant vertebrates from San Salvador (Watling's) Island, Bahamas. Smithsonian Contributions to Zoology 508: 1–15.

Orihuela, J. 2012. Skull variation of the vampire bat *Desmodus rotundus* (Chiroptera: Phyllostomidae): taxonomic implications for the Cuban fossil vampire bat *Desmodus puntajudensis*. Chiroptera Neotropical 17: 863–876.

Pardiñas, U.F.J., and E.P. Tonni. 2000. A giant vampire (Mammalia, Chiroptera) in the Late Holocene from the Argentinean pampas: paleoenvironmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology 160: 213–221.

Paula Couto, C. 1946. Atualização da nomenclatura genérica e específica usada por Herluf Winge em "E Museo Lundii." Estudos Brasileiros de Geologia 1: 59–80.

Pavan, A.C., F.M. Martins, and J.S. Morgante. 2013. Evolutionary history of bulldog bats (genus *Noctilio*): recent diversification and the role of the Caribbean in Neotropical biogeography. Biological Journal of the Linnean Society 108: 210–224.

Peracchi, A.L., I.P. Lima, M.R. Nogueira, and H. Ortêncio Filho. 2011. Ordem Chiroptera. *In* N.R. Reis, A.L. Peracchi, W.A. Pedro, and I.P. Lima (editors), Mamíferos do Brasil, 2nd ed.: 155–234. Londrina: N.R. Reis.

Prado, D.E. 2003. As caatingas da América do Sul. *In* I. Leal, M. Tabarelli, and J. Silva (editors), Ecologia e conservação da Caatinga: 3–73. Recife: Editora Universitária – UFPE.

Pregill, G.K., D.W. Steadman, and D.R. Watters. 1994. Late Quaternary vertebrate faunas of the Lesser Antilles: historical components of Caribbean biogeography. Bulletin of the Carnegie Museum of Natural History 30: 1–51.

Reynolds, T.E., K.F. Koopman, and E.E. Williams. 1953. A cave faunule from western Puerto Rico with a discussion of the genus *Isolobodon*. Breviora 12: 1–8.

Rezsutek, M., and G.N. Cameron. 1993. *Mormoops megalophylla*. Mammalian Species 448: 1–5.

Rincón, A.D. 1999. Los pequeños mamíferos subfósiles presentes en cuevas de la Sierra de Perijá, Estado Zulia, Venezuela. El Guácharo, Boletín Espeleológico 48: 1–75.

Rocha, W.J.S.F., J.M. Chaves, C.C. Rocha, L. Funch, and F.A. Juncá. 2005. Avaliação ecológica rápida da Chapada Diamantina. *In* F.A. Juncá, L. Funch, and W. Rocha (editors), Biodiversidade e conservação da Chapada Diamantina: 377–405. Brasília: Ministério do Meio Ambiente.

Salles, L.O., et al. 1999. Mammals from the Quaternary of Serra da Mesa (Goiás, Brazil). Publicações Avulsas do Museu Nacional 78: 1–15.

Santos, A.M.M., D.R. Cavalcanti, J.M.C. Silva, and M. Tabarelli. 2007. Biogeographical relationships among tropical forests in north-eastern Brazil. Journal of Biogeography 34: 437–446.

Sá-Neto, R.J., and Marinho-Filho, J. 2013. Bats in fragments of xeric woodland caatinga in Brazilian semiarid. Journal of Arid Environments 90: 88–94.

Sbragia, I.A. 2012. Composição, distribuição, aspectos taxonômicos e citogenéticos da quiropterofauna da Chapada Diamantina, Bahia. Ph.D. dissertation, Museu Nacional, Universidade Federal do Rio de Janeiro. 245 pp.

Silva Taboada, G. 1974. Fossil Chiroptera from cave deposits in central Cuba, with description of two new species (Genera *Pteronotus* and *Mormoops*) and the first West Indian record of *Mormoops megalophylla*. Acta Zoologica Cracoviensia 19: 33–73.

Silva Taboada, G. 1979. Los murcielagos de Cuba: taxonomía, morfología, distribución, biogeografía, importancia económica. Havana: Editorial Científico-Tecnica.

Simmons, N.B. 2005. Order Chiroptera. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, a taxonomic and geographic reference: 312–529. Baltimore: Johns Hopkins University Press.

Simmons, N.B., and R.S. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna, part 1. Bats. Bulletin of the American Museum of Natural History 237: 1–219.

Souza, S.L., P.C.R. Brito, and R.W.S. Silva. 1993. Estratigrafia, sedimentologia e recursos minerais da Formação Salitre na Bacia de Irecê, Bahia. Companhia Baiana de Pesquisa Mineral. Salvador: Série Arquivos Abertos 2.

Swartz, S.M., J. Iriarte-Díaz, D.K. Riskin, and K.S. Breuer. 2012. A bird? A plane? No, it's a bat: an introduction to the biomechanics of bat flight. *In* G.F. Gunnell and N.B. Simmons (editors), Evolutionary history of bats: fossils, molecules, and morphology: 317–352. Cambridge: Cambridge University Press.

Trajano, E., and M. de Vivo. 1991. *Desmodus draculae* Morgan, Linares, and Ray, 1988, reported for southeastern Brazil, with paleoecological comments (Phyllostomidae, Desmodontinae). Mammalia 55: 456–459.

Velazco, P.M., et al. 2013. Quaternary bat diversity in the Dominican Republic. American Museum Novitates 3779: 1–20.

Voss, R.S., and L.H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History 230: 1–115.

Wetterer, A.L., M.V. Rockman, and N.B. Simmons. 2000. Phylogeny of phyllostomid bats (Mammalia: Chiroptera): data from diverse morphological systems, sex chromosomes, and restriction sites. Bulletin of the American Museum of Natural History 248: 1–200.

Winge, H. 1892. Jordfundne og nulevende Flagermus (Chiroptera) fra Lagoa Santa, Minas Geraes, Brasilien: med udsigt over Flagermusenes indbyrdes Slaegtskab. E Museo Lundii 2: 1–92.

APPENDIX 1

EXTANT SPECIMENS EXAMINED

Specimens of extant bats used for taxonomic comparisons are listed below. Institutional acronyms are as follows: ALP, Adriano Lúcio Peracchi Collection, Universidade Federal Rural do Rio de Janeiro (UFRRJ) (Rio de Janeiro); AMNH, American Museum of Natural History (New York); MN, Museu Nacional, Universidade Federal do Rio de Janeiro (Rio de Janeiro); and MZUSP, Museu de Zoologia da Universidade de São Paulo (São Paulo).

FAMILY EMBALLONURIDAE
   Peropteryx macrotis: AMNH 91237.
   Taphozous georgianus: AMNH 197177.
   Taphozous melanopogon: AMNH 235571.

FAMILY PHYLLOSTOMIDAE
   Chrotopterus auritus: MN 46484; MN 56248.
   Phyllostomus hastatus: AMNH 99607; AMNH 209334; AMNH 230171; AMNH 267901;
   ALP 2287; MN 5167; MN 25708; MN 37330; MN 47235; MN 47236; MN 56238.
   Tonatia bidens: MN 43083; MZUSP 22569.
   Trachops cirrhosus: AMNH 267932; MN 50063.
   Vampyrum spectrum: MN 46499.

FAMILY MORMOOPIDAE
   Mormoops blainvillei: AMNH 238144.
   Mormoops megalophylla: AMNH 25602.
   Pteronotus davyi: AMNH 203565.
   Pteronotus gymnonotus: ALP 9039.
   Pteronotus macleayii: AMNH 60917.
   Pteronotus parnellii: AMNH 254607; MN 36636; MN 37108; MN 37110; MN 37112.
   Pteronotus personatus: AMNH 178468; ALP 9091.
   Pteronotus quadridens: AMNH 39405.

FAMILY NOCTILIONIDAE
   Noctilio albiventris: AMNH 210594; MN 60520; ALP 2880.
   Noctilio leporinus: AMNH 256528; MN 47200; MN 47201; MN 47204.

FAMILY FURIPTERIDAE
   Amorphochilus schnablii: AMNH 28601.
   Furipterus horrens: MN 36057.

FAMILY THYROPTERIDAE
   Thyroptera tricolor: AMNH 266361; MN 46443.

FAMILY NATALIDAE
   Natalus stramineus: MN 43104; MN 59843.

FAMILY VESPERTILIONIDAE
   Antrozous pallidus: AMNH 207615; AMNH 274878.
   Bauerus dubiaquercus: AMNH 256832.
   Histiotus montanus: AMNH 205649.
   Histiotus velatus: MN 3373; MN 46450.
   Myotis albescens: AMNH 234361.

APPENDIX 2

Fossil Specimens Examined

Specimens of fossil humeri examined in this study are listed below, with details about state of preservation abbreviated as follows: *ch*, complete humerus; *ps*, proximal humerus with part of the shaft preserved; *p*, proximal fragment only; *ds*, distal humerus with part of the shaft preserved; and *d*, distal fragment only. All specimens are deposited in the Museu Nacional, Universidade Federal do Rio de Janeiro (Rio de Janeiro), abbreviated as MN.

FAMILY PHYLLOSTOMIDAE

   Chrotopterus auritus: MN 57430 (ch).

FAMILY MORMOOPIDAE

   Mormoops cf. *megalophylla*: MN 57402 (ch); MN 57403 (ch); MN 57404 (ps); MN 57405 (ps); MN 57406 (ch); MN 57407 (ch); MN 57408 (ds); MN 57409 (ds); MN 57410 (ps).
   Pteronotus gymnonotus: MN 57411 (ch); MN 57412 (ds); MN 57413 (ch); MN 57414 (ds); MN 57415 (ds); MN 57416 (ps); MN 57417 (p).
   Pteronotus parnellii: MN 57418 (ds); MN 57419 (d); MN 57420 (ch); MN 57421 (ch); MN 57422 (ch); MN 57423 (ch); MN 57424 (ch); MN 57425 (d); MN 57426 (ps); MN 57427 (ds); MN 57428 (ch).

FAMILY NOCTILIONIDAE

   Noctilio leporinus: MN 57400 (ch); MN 57401 (ch).

FAMILY FURIPTERIDAE

   Furipterus horrens: MN 57429 (d).